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MAHOGANY (*Swietenia*) HYBRIDS

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RESUMEN

Este estudio concluye que *Swietenia macrophylla* x *mahagoni* es lo mismo que *S. aubrevilleana* Stehlé & Cusin y que es un híbrido merecedor de pruebas extensivas para adaptabilidad. Dos nuevos híbridos putativos, *S. humilis* x *macrophylla* y *S. humilis* x *mahagoni*, están descritos. *S. humilis* x *macrophylla* (?) ocurre naturalmente en el noroeste de Costa Rica y es intermedio en cuanto a crecimiento en altura, supervivencia en sitios húmedos, características foliares, y altura, diámetro y altura de las gambas de árboles maduros. El peso de las semillas, número de hojuelas y supervivencia en sitios secos son mayores que en las especies padres. *S. humilis* x *mahagoni* (?) ocurre donde las dos especies están sembradas juntas y es intermedio en crecimiento, en altura, peso de las semillas, largo y ancho de las hojas simples, tanto como las hojuelas de hojas compuestas (número de hojuelas por hoja asemeja más la sospechada fuente de polen, *S. mahagoni*). Este híbrido putativo demuestra crecimiento juvenil superior al de *S. macrophylla* x *mahagoni*.

SUMMARY

This study concludes that *Swietenia macrophylla* x *mahagoni* is the same as *S. aubrevilleana* Stehlé & Cusin and is a hybrid worthy of widespread adaptability trials. Two new putative hybrids, *S. humilis* x *macrophylla* and *S. humilis* x *mahagoni*, are described. *S. humilis* x *macrophylla* (?) occurs naturally in northwestern Costa Rica and is intermediate between the parent species in height growth, survival on wet sites, leaf characteristics, and height, diameter, and buttress height of mature trees. Seed weight, leaflet number, and dry site survival are greater than those of either parent. *S. humilis* x *mahagoni* (?) occurs where the two species are planted in proximity and is intermediate between the parent species in height growth, seed weight, length and width of simple leaves as well as later leaflets (number of leaflets per leaf is more like that of the suspected pollen parent). This putative hybrid shows juvenile growth superior to that of *S. macrophylla* x *mahagoni*.

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MAHOGANY (*SWIETENIA*) HYBRIDS¹

By J.L. Whitmore² and Gilberto Hinojosa³

The genus *Swietenia* (Meliaceae), source of all western hemisphere or true mahogany, is recognized by most authorities to have only three species. *S. mahagoni* Jacq. (West Indies mahogany) is native to the Greater Antilles (except Puerto Rico), the Bahamas, and the southern tip of Florida, a series of populations isolated from each other and from the other two species' ranges. *S. macrophylla* King (Honduras mahogany) has a more continuous range, extending along the mainland from Mexico to Bolivia. *S. humilis* Zucc. (Pacific Coast mahogany) is found in a narrow band along the Pacific Coast between Puntarenas, Costa Rica, and Sinaloa, Mexico, with a disjunct patch in eastern Guatemala, west-southwest of Lake Izabal. The ranges of *S. macrophylla* and *S. humilis* overlap in at least three areas: Mexico (Tehuantepec), Guatemala, and Costa Rica (Lamb, 1966).

S. macrophylla x *mahagoni* is an important hybrid being tried in several countries because of its form, growth rate, drought resistance, and wood quality. Two putative hybrids, *S. humilis* x *macrophylla* and *S. humilis* x *mahagoni*, are relatively unknown and untested. This study clarifies taxonomically the previously known *Swietenia macrophylla* x *mahagoni*, describes the two new putative hybrids, and comments on the theoretical relationships of the three species. We made seed counts of the three species and their hybrids in the laboratory and compared their performance in the nursery and field via tests in Puerto Rico and Costa Rica. In addition, earlier studies by other researchers were reviewed and reinterpreted.

S. macrophylla x *mahagoni*

The only previously described interspecific hybrid of *Swietenia* is *S. macrophylla* x *mahagoni*. The result of planting both species in proximity, this hybrid was discovered in Puerto Rico in 1935. It has more drought resistance (Nobles and Briscoe, 1966) and better wood quality than *S. macrophylla* and grows faster on some sites than either parent (Briscoe and Nobles, 1962; Lamb, 1966; Geary *et al.*, 1972). The hybrid also has better form than *S. mahagoni* (Fig. 1). It is easily distinguished from either parent by its intermediate leaf size (Fig. 2).



Figure 1. Fifteen-year-old plantation of *Swietenia macrophylla* x *mahagoni* in St. Croix, U.S. Virgin Islands.

Seed weight is also intermediate (Table 1). In Puerto Rico and Saint Croix, Virgin Islands—where *S. mahagoni* is seldom attacked by the *Hypsipyla grandella* Zeller shootborer and *S. macrophylla* is highly susceptible⁴ (Geary *et al.*, 1973)—the hybrid appears to be more resistant to borer attack than is *S. macrophylla*. Because of these qualities, this hybrid merits tropics-wide attention and adaptability testing.

S. macrophylla and *S. mahagoni* are the only mahogany species to be hybridized artificially (Lee, 1968). This feat was initially difficult, however, because their flowers are minute and their floral biology and morphology were only recently understood (Lamb, 1960; 1966; Yang, 1965; Lee, 1967; Styles, 1972).

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⁴In Haiti the opposite is true. The borer prefers *S. mahagoni*, which is native to Haiti, and refuses *S. macrophylla*. This indicates that the insect and *S. mahagoni* have evolved together in Haiti and supports the conclusion that *S. mahagoni* is not native to Puerto Rico since the insect does not attack it. Apparently, the insect has not evolved a taste for the species in some 200 years since the tree was introduced in Puerto Rico.

Table 1. Number of de-winged seeds per kilo of *Swietenia* species and hybrids.
Virgin Islands sources are plantations.

Species or hybrid	# seeds/k	Origin
<i>S. macrophylla</i>	2100	Belize
<i>S. macrophylla</i> x <i>mahagoni</i>	2880	Virgin Islands (St. Croix)
<i>S. mahagoni</i> ^{a/}	7840	Virgin Islands (St. Croix)
<i>S. humilis</i> x <i>mahagoni</i> (?)	1960	Virgin Islands (St. Croix)
<i>S. humilis</i> ^{b/}	1540	Mexico (Guerrero)
<i>S. humilis</i> x <i>macrophylla</i> (?)	2360	Costa Rica (Guanacaste)

a/*S. mahagoni* from St. Croix, birdseye variety, had 11330 seeds per kilo.

b/*S. humilis* from St. Croix (used in nursery and field trials described in the text) had 1660 seeds per kilo.

We conclude that this intermediate mahogany is the same which Stehlé & Cusin described as a new species, *S. aubrevilleana* (Stehlé, 1958) since intermediate forms have been found only where mature stands of both species are together and only in areas where early botanical exploration showed no trace of an intermediate form. Thus, the binomial may be designated as *Swietenia* x *aubrevilleana* Stehlé & Cusin. However, we prefer the formula *Swietenia macrophylla* x *mahagoni* for reasons stated by Little (1960).



Figure 2. Leaves of *Swietenia macrophylla*, *S. macrophylla* x *mahagoni*, and *S. mahagoni* (left to right).

S. humilis x *macrophylla* (?)

Field workers find it difficult to distinguish between *S. macrophylla* and *S. humilis*. This confusion is especially serious where their natural distributions meet. One such area is northwestern Costa Rica. In this habitat with a strong dry season typical of *S. humilis*' natural range, the mahogany's morphological characters are quite variable but tend to resemble those of *S. humilis* (Fig. 3). The hybrid character of this mahogany has been suspected by local foresters and is supported by the findings of Geary *et al.* (1973). They report a population near Liberia, Guanacaste, that falls between *S. humilis* and *S. macrophylla* in survival at wet sites, annual height growth, rachis length, leaflet length and width, and height, diameter, and buttress height of mature trees. It survives better than either species on dry sites and has a greater number of leaflets than either species.

Our recent collections from the Puntarenas and Santa Rosa National Park (Guanacaste) areas also



Figure 3. Leaf and fruit size of *Swietenia humilis* x *macrophylla* (?) from northwestern Costa Rica. Large fruits and small leaves are from a tree near Santa Rosa Park, Guanacaste (A). Trees with highly variable leaf size and shape are found in a pasture in Puntarenas (B). Scale is in centimeters.

indicate hybridization. These collections show a mean seed capsule length of 13.5 cm; Geary *et al.* (1973) found mean seed capsule lengths of 13.9 for *S. macrophylla* and 13.0 cm for *S. humilis*. We found a seed weight greater than that of either species but closer to that of *S. macrophylla* (Table 1), and a highly variable leaflet size and shape (Fig. 3). Most likely, both species are present in Puntarenas and Guanacaste, and some populations there represent hybrid swarms. Much of the *Swietenia* seed collected in Costa Rica in past years has been from Guanacaste and Puntarenas and has been labeled either *S. humilis* or *S. macrophylla*. However, at least some of it might better be called a putative hybrid, *S. humilis* x *macrophylla*, based on our observations and those of Geary *et al.* (1973).

Geary *et al.* (1973) also found a source from the south coast of Guatemala which they labeled *S.*

humilis but which actually resembles *S. macrophylla* more than *S. humilis*. That area is well out of the *S. macrophylla* range and into the *S. humilis* range as we know these ranges. Possibly the present range map of *S. macrophylla* in Guatemala (Lamb, 1966) is wrong and hybridization is occurring between the two species in the south coast area.

Boone and Chudnoff (1970) studied the specific gravity of mahoganies from 24 areas in Mexico, Central America and Panamá, including the Guanacaste and south-coast Guatemala areas. They found the heartwood specific gravity of *S. macrophylla* to average 0.61, that of *S. humilis* 0.78, and the range in the two areas in question 0.68—0.74. Sapwood follows the same pattern. These data support the theory that hybridization is occurring in both NW Costa Rica and in south-coast

Guatemala.

Wright (1962) stresses the need to grow new hybrid combinations in replicated nursery trials to detect male characters in them as well as using controlled pollination techniques before certification as hybrids. Unfortunately, no controlled pollination has been attempted between these two species, and we can't identify the male parent of field specimens. The need for intensive studies on Costa Rican, and perhaps Guatemalan, populations of mahogany is obvious.

S. humilis x *mahagoni* (?)

S. humilis x *mahagoni* has not been observed before, to our knowledge. The ranges of the two parent species are distinct and distant from each other, and apparently no one has attempted to artificially hybridize them. However, *S. humilis* has been sown in trial plots adjacent to *S. mahagoni*, and in Saint Croix one such trial plot of *S. humilis* first bore fruits in March 1972, eleven years after outplanting.

Theoretically, at least some of the resulting seeds were products of *S. mahagoni* pollen (carried by insects, according to Styles, 1972). Fruits of these young trees were collected in early 1973 to study the resulting seedlings under Puerto Rico nursery and field conditions.

Seed weight fell between that of the two species (Table 1). Measurement in the Río Piedras nursery showed these seedlings to be between *S. humilis* and *S. mahagoni* in height and in length and width of the largest simple leaf (prior to or concurrent with emergence of the first compound leaves). The number of compound leaves per seedling was greater for the supposed hybrid than for either parent (Table 2).

On 19 September 1973, these seedlings were outplanted at Vieques, Puerto Rico, on a site with droughty granitic sand soil, a long dry season, and annual rainfall of about 1000 mm. Later measurements showed the supposed hybrids to be between the two species in height and in length and width of the largest leaflets (Table 3). Some traits resembled the suspected male parent more than the female parent, for example, number of leaflets per leaf and early field height. These measurements suggest that the seedlings represent a hybrid population rather than pure *S. humilis*.

S. humilis has prominent lateral veins but *S. mahagoni* does not (Briscoe and Lamb, 1962). The Vieques plantation tended to confirm this distinction, and the putative hybrid plants had lateral veins which varied from inconspicuous to obvious. Venation in *Swietenia* could prove a

valuable tool in distinguishing between the species and their hybrids. However, until this parameter can be quantified, it must be considered subjective and vague. Also, prominence of veins appears to correlate well with leaf size: smaller *S. humilis* leaves have less conspicuous veins than larger leaves of the same species.

In further nursery trials in Puerto Rico, the supposed hybrid was found to fall between both species in height, early compound leaf formation, and length and width of the largest simple leaf. In root pattern it was more similar to the suspected pollen parent: both formed long taproots rather than the ball-root system of the nursery stage *S. humilis*.

Another trial was installed in a Turrialba, Costa Rica, nursery using the March 1974 seed crop of the same young St. Croix tree plus two others: *S. macrophylla* and *S. macrophylla* x *mahagoni*. This trial showed the supposed *S. humilis* x *mahagoni* hybrid to be intermediate between both parents in height growth, as was the *S. macrophylla* x *mahagoni*. *S. humilis* x *mahagoni* (?) outgrew the better-known *S. macrophylla* x *mahagoni* in the nursery stage by a large margin (Table 4).

Species of *Swietenia*

Pennington and Styles (1975) consider the genus to consist of three "poorly defined" species, *mahagoni*, *macrophylla*, and *humilis*. Chromosome numbers for the three are $2n=48$, 54 and 56, respectively (Styles and Vosa, 1971). J.A. Tosi of the Tropical Science Center, San José, Costa Rica (personal communication) suggests that *macrophylla* and *humilis* may simply be ecotypes of the same species. Perhaps the more likely, although also unproven as yet, theory is that of F. Bascopé of the Bolivian Renewable Natural Resources Service (personal communication); he feels that *Swietenia* may be monotypic.

It may well be that all three presently-recognized species should be considered one or that *Swietenia* is in a less than complete process of speciation with only two groups, insular (plus the tip of Florida) and continental, fairly well defined. Either idea can be supported by the findings of this study, which indicate the ease of hybridization between all species or population groups. Both ideas raise the questions of intraspecific hybrids and intraspecific chromosome variability. But until further work is done which specifically approaches the problem of "poorly defined" species of *Swietenia*, it will be necessary to accept the concept of three distinct species.

Table 2: Mean heights and leaf characters of three Swietenia populations in the nursery stage. Design used 48-tree plots, four randomized complete blocks.^{a/}

Population	Height means (cm) 12 July 1973	Leaf characters 15 - 20 August 1973		
		# of compound leaves per tree	Means of largest simple (juvenile) leaves (mm) Length	Width
<u>Swietenia humilis</u> ^{b/}	15.6 a	3.6 a	88.9 a	38.9 a
<u>S. humilis</u> x <u>mahagoni</u> (?)	13.3 b	5.8 b	75.4 b	33.5 b
<u>S. mahagoni</u> ^{b/}	7.8 c	4.4 a	46.6 c	13.8 c

^{a/} Within columns, means followed by different letters are significantly different at the 0.05 level according to ANOVA and Duncan's multiple range test.

^{b/} From trees growing on St. Croix, believed to be pure. Seed from the native range was not available. The S. humilis seed came from a single, isolated tree.

Table 3. Mean heights and leaf characters of three Swietenia populations outplanted in Vieques, Puerto Rico, 19 September 1973.^{a/}

Population	Height means ^{b/} (cm)		Leaf Characters # of leaflets per leaf ^{c/}	March 1974 Mean of largest leaflets (cm) ^{d/}	
	6 Feb. 1974	8 Jan. 1975		Length	Width
<u>S. humilis</u> ^{e/}	24.0 a	53.0 a	5.1 a	10.5 a	4.1 a
<u>S. humilis</u> x <u>mahagoni</u> (?)	18.2 b	39.7 b	6.5 b	7.7 b	2.9 b
<u>S. mahagoni</u> ^{e/}	18.5 b	35.8 c	6.4 b	3.9 c	1.3 c

^{a/} Within columns, means followed by different letters are significantly different at the 0.05 level according to ANOVA and Duncan's multiple range test.

^{b/} Design used 48-tree plots, four randomized complete blocks.

^{c/} From a sample of 66 leaves per population.

^{d/} No of leaflets measured varies between 64 and 90 per population: the two largest leaflets of all compound leaves on 6 to 8 trees per population were measured in two replicates.

^{e/} From trees growing on St. Croix, believed to be pure. Seed from the native range was not available. The S. humilis seed came from a single, isolated tree.

Table 4. Growth variation among five Swietenia populations in the Turrialba nursery. Seeds were sown 10 and 11 September 1974. Design used 84 tree plots, 7 blocks^{a/}.

Population	7 Oct. 1974	Mean height (cm)	
		23 Oct. 1974	6 Dec. 1974
<u>Swietenia humilis</u>	6.8 a	11.0 a	15.3 a
<u>S. humilis</u> x <u>mahagoni</u> (?)	5.9 b	9.1 b	12.0 b
<u>S. macrophylla</u>	5.5 b	6.5 c	8.2 c
<u>S. macrophylla</u> x <u>mahagoni</u>	2.7 c	5.1 d	7.7 c
<u>S. mahagoni</u>	2.3 c	2.8 e	4.7 d

^{a/} Within columns, means followed by different letters are significantly different at the 0.05 level according to ANOVA and Duncan's multiple range test.

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Retrieval Terms: Meliaceae, tropical silviculture, taxonomy, tree improvement, genetic variation.

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